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THE TAXONOMIC STATUS OF COYOTES FROM
WESTERN SOUTH DAKOTA

BY

SUSAN E. LAUZON

A thesis submitted
in partial fulfillment of the requirements for the
degree Master of Science, Major in
Wildlife and Fisheries Sciences,
South Dakota State University

1979

THE TAXONOMIC STATUS OF COYOTES FROM
WESTERN SOUTH DAKOTA

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable as meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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ABSTRACT

Expansion of the range of the coyote (Canis latrans) has been accompanied by numerous instances of hybridization with domestic dogs (C. familiaris). Recent studies have found a hybrid element in some wild coyote populations. The objectives of this study were to identify the taxonomic status of coyotes in western South Dakota, and to determine the degree of hybridization, if any, that is occurring between coyotes and domestic dogs in the state. Animals were collected from three areas in western South Dakota from September 1976 through January 1978. Skulls of 289 wild canids were cleaned; of these, 167 skulls from adults of known sex were suitable for analysis. Seven cranial and tooth measurements were taken on each skull. Discriminant function analysis and canonical variable analysis were used to determine the taxonomic status of specimens. Each specimen was compared to six target populations of possible parent species. No specimens analyzed could be positively identified as anything other than coyotes. Five individuals were of undetermined taxonomic status. The reason for the lack of hybrids in South Dakota coyote populations may be either that hybrids are not surviving in the wild or that hybridization is not occurring on a large scale. The two hypotheses are considered, and it is concluded that hybridization is not occurring to any great extent in western South Dakota coyote populations.

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INTRODUCTION

The range of the coyote (Canis latrans) has been steadily expanding (Young and Jackson 1951). This expansion has been accompanied by numerous instances of hybridization with domestic dogs (C. familiaris). Reports of coyote-dog crosses have come from within the original range of coyotes (Bee and Hall 1951, Young and Jackson 1951, Gier 1968), as well as from areas recently occupied by coyotes (Aldous 1939, Pringle 1960). The frequent capture of canids that were difficult to identify, and presumably hybrids, led to the speculation that "coydogs" would become an important element in wild canid populations (Cook 1952).

Studies of coyote-dog hybrids kept in captivity raised the question of whether or not these animals could become a viable component in wild populations. The first study of captive coyote-dog hybrids (Dice 1942) led to the conclusion that these hybrids were most likely sterile, and could not become established in wild populations. On the basis of the little work that had been done at that time, Hall (1943) speculated that hybrids might be unable to live to even one year of age. Later studies of captive animals (Kennelly and Roberts 1969, Silver and Silver 1969, Mengel 1971) showed that coyote-dog hybrids were not only fertile, but could survive to maturity. Infertility in interspecific hybrids often results from too great a difference in parental karyotypes (Benirschke 1967). Since coyotes

and dogs have identical karyotypes ($2N=78$), such infertility should not occur in their hybrid offspring.

Coyotes have a single annual breeding season, generally considered to be from early January to mid-March (Young and Jackson 1951, Gier 1968). It was once thought that male coyote-dog hybrids were not seasonal breeders, but produced sperm year-round, as dogs do (Kennelly and Roberts 1969). If this were the case, male hybrids could easily mate with both coyotes and dogs. However, research on the reproductive characteristics of coyote-dog hybrids contradicted this, and brought into question the likelihood of hybrids becoming established in a wild population. Silver and Silver (1969) and Mengel (1971) found that hybrids were actually seasonal breeders, but with a breeding season two to three months earlier than that of coyotes. On the basis of this information it was felt that there was no chance of hybrids back-crossing with coyotes. The non-synchronous breeding seasons of the two groups indicated there could be little or no introgression of dog genes into the coyote gene pool. Gipson (1972) and Gipson et al. (1975) reported data that contradicts this hypothesis. Male coyotes were found that were reproductively active as early as late November, and male hybrids were capable of breeding through January. This indicates that male coyotes could mate with female hybrids, and male hybrids could mate with early-breeding female coyotes. Based on these facts, the filtering of dog genes into coyote populations as a result of hybrids breeding with coyotes seems possible. Studies in Oklahoma

(Freeman 1976) and Nebraska (Mahan et al. 1978) suggest that such back-crossing of hybrids with coyotes may in fact be occurring in the wild.

Early attempts to identify the taxonomic status of canids were often subjective and unreliable. Dice (1942) reported the skull characters of his pen-reared hybrids simply as being broader in all areas than coyote skulls. The series of skull characters analyzed by Hall (1943) were reported in relative terms: small, intermediate, or large, etc. The accuracy of the "skull ratio," a measurement that could be made with a ruler or a stick in the field (Howard 1949), is questionable. Bee and Hall (1951) measured the skulls of three coyote-dog hybrids, using the orbital angle described by Iljin (1941), and three other indices of skull measurements. When Richens and Hugie (1974) identified Maine wild canids as a separate race of coyotes, rather than hybrids, they did so on the basis of relative body size and skull measurements which consisted of zygomatic width, canine size, condylobasal length, and Howard's (1949) skull ratio. The confusion as to the taxonomic status of canids in various areas may well be a result of this lack of a uniform set of characteristics used to classify individuals.

Lawrence and Bossert (1967), using linear discrimination similar to that described by Jolicoeur (1959), began with 42 characters of known value in distinguishing between the wolf (C. lupus), coyote, and dog. Of these, the 24 most discriminative measurements were selected, and finally 16 measurements (ten cranial and six tooth measurements)

were found to be the most diagnostic. It was possible to significantly distinguish between the three species using this technique. Lawrence and Bossert (1969) later used this same technique to show that coyote-dog hybrids clearly fall between the two parent stocks in such a multiple character analysis, and can be readily identified using this method. Gipson (1972) and Gipson et al. (1974) further refined this technique, and Mahan et al. (1978) ultimately chose seven variables which were the optimum set of measurements required for discrimination. These more recent multivariate analysis techniques provide the most accurate method to date for consistently identifying the taxonomic group to which an animal belongs.

Silver and Silver (1969) and Mengel (1971) found that male parental behavior in hybrids differed from typical coyote behavior. Mengel (1971) reported that all of his captive coyote-dog hybrids were more aggressive than dogs, and Silver and Silver (1969) reported hybrids to be less timid than coyotes. Gipson (1972) also reported that some wild hybrids were more aggressive than coyotes. This, and their greater tendency than coyotes to run in packs (Freeman 1976), indicates behavioral differences between hybrids and their parental stock. Coyote-dog hybrids in a wild population could exhibit behavior that varies enough from pure coyotes to warrant a change in coyote damage control techniques.

South Dakota is within the historic range of the coyote. Considerable time and effort have been expended on the control of coyote damage within the state. Free-ranging dogs in western areas of South

Dakota could mate with coyotes frequently enough to enable establishment of a hybrid element in the wild canid population. If this were the case, the altered behavior of the animals could be important enough to demand a shift in predator damage control and/or livestock management techniques.

The objectives of this study were to identify the taxonomic status of coyotes in western South Dakota, and to determine the degree of hybridization, if any, that has occurred between coyotes and domestic dogs in the state.

MATERIALS AND METHODS

Wild canids were collected from three areas in South Dakota. These included Harding County in the extreme northwestern corner of the state, Custer and Fall River Counties in southwestern South Dakota (Black Hills region), and Gregory and Tripp Counties on the southern border of the state immediately west of the Missouri River (Figure 1). All three collection areas were located west of the Missouri River; this half of the state is primarily rangeland, and is often considered South Dakota's prime coyote habitat.

Canids were collected from September 1976 through January 1978. Carcasses were obtained with the assistance of furbuyers and state trappers. All animals were either necropsied while fresh, or frozen for later examination. Before cleaning, skulls were stored either frozen or in a dermestid chamber.

All skulls were cleaned by boiling in a pressure cooker at five to seven pounds pressure for approximately 45 minutes, or until clean.

Undamaged skulls of all adult canids of known sex were measured. Pups were identified by the presence of an open root canal in the canine teeth. Skulls with a closed canine root canal were considered nine months of age or older (Linhart and Knowlton 1967) and were classified as adults for the purpose of this study.

Skull measurements were made to the nearest 0.05 mm with dial calipers. Seven cranial and tooth measurements, which have been determined to be the most diagnostic characteristics for use in discriminant

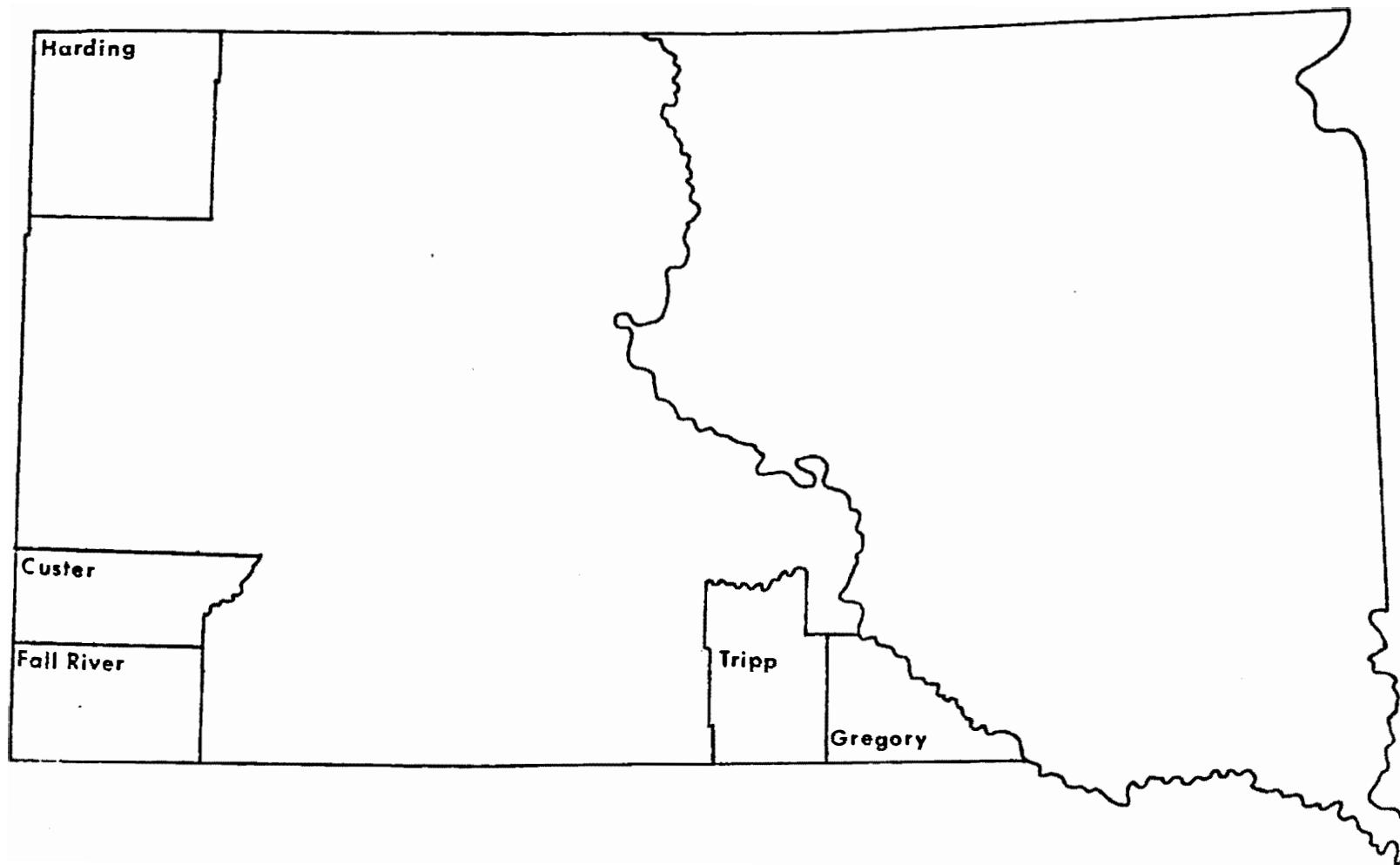


Figure 1. Map of South Dakota showing the three areas of specimen collection.

analysis (Mahan et al. 1978), were taken on each adult skull. The measurements used (Figure 2) were as follows: 1) zygomatic width; 2) maximum crown width of second upper molar (M^2); 3) maximum crown width across upper cheek teeth; 4) minimum crown width of fourth upper premolar (PM^4) taken between roots; 5) minimum width between alveoli of first upper premolars (PM^1); 6) maximum crown width across upper incisors (I); 7) maximum antero-posterior width of upper canine (C) taken at base of enamel. Some of these measurements were combined as ratios for use in the analysis. The complete set of measurements and ratios analyzed (using measurements numbered as above) consisted of: 1; 3; 4; 3 divided by 2; 5 divided by 2; 6 divided by 2; and 7 divided by 2.

Specimens were classified using discriminant function analysis and canonical variable analysis. Each skull was compared to target populations of skulls from known coyotes, dogs, coyote-dog hybrids, red wolves (C. rufus), timber wolves (C. lupus lycaon), and prairie wolves (C. lupus nubilus and C. l. monstrabilis). Data for the target populations were provided by P. S. Gipson (Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks).

Multivariate analysis is used to distinguish between groups which may overlap with respect to any single characteristic. Simultaneous analysis of a combination of variables makes it possible to statistically separate groups more completely than if only one character were used. The discriminating variables used in the analysis are weighted and linearly combined. These linear combinations, or discriminant

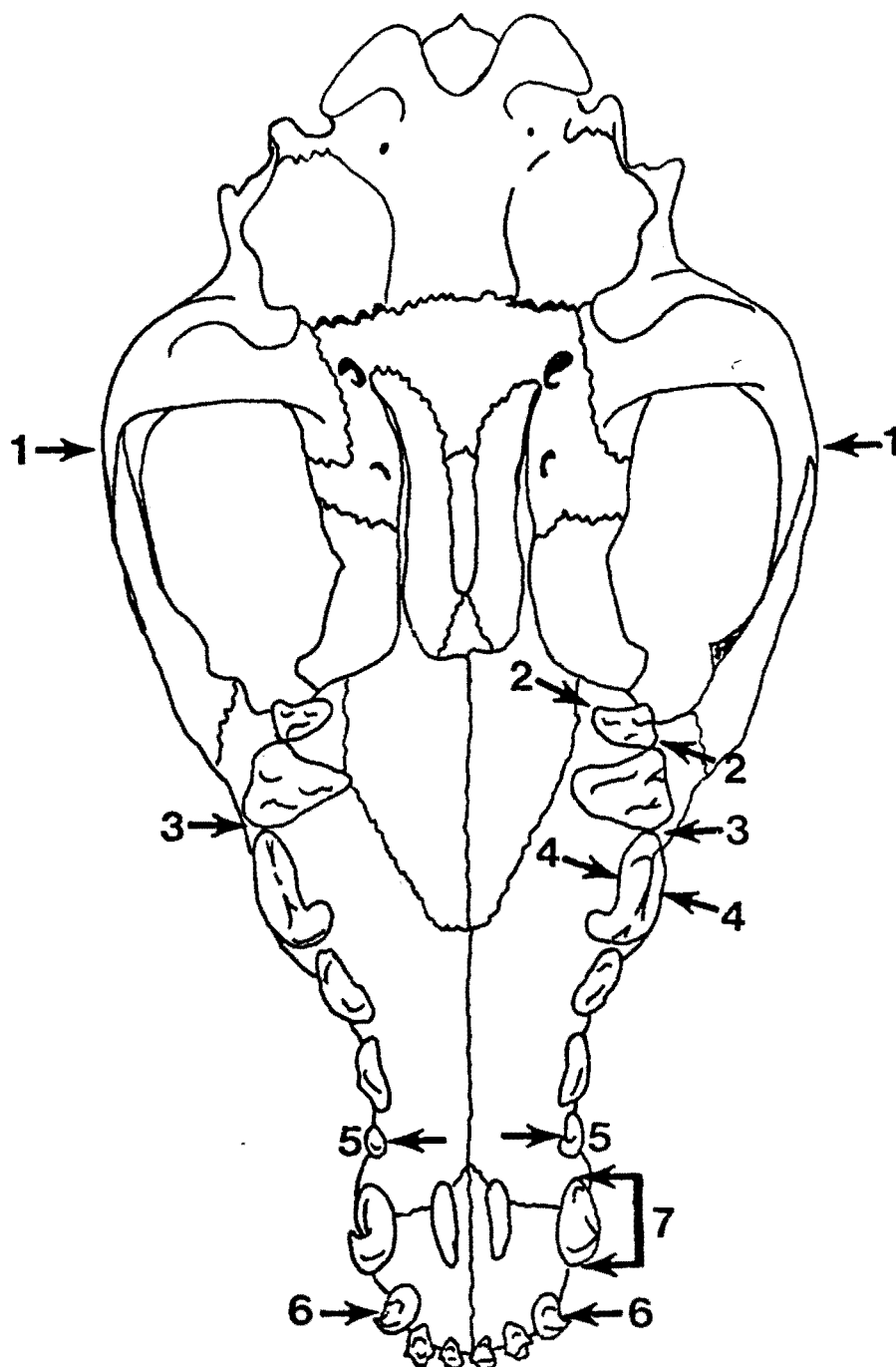


Figure 2. Canid skull measurements used in discriminant analysis.

- 1: zygomatic width
- 2: maximum crown width of second upper molar
- 3: maximum crown width across upper cheek teeth
- 4: minimum crown width of fourth upper premolar
- 5: minimum width between alveoli of first upper premolars
- 6: maximum crown width across upper incisors
- 7: maximum antero-posterior width of upper canine

functions, are formed so as to provide maximum separation between the groups. Satisfactory discrimination was provided in this study by three discriminant functions, that is, three linear combinations of the seven discriminating variables.

Canonical variable analysis (Rao 1952) allowed visual representation of the taxonomic classification of specimens. The canonical variables of each animal were calculated and plotted on a graph showing the 95 percent confidence limits of each target population. Each individual could then be seen in relation to all six of its possible parent populations, and the taxonomic status of each specimen could be determined according to where it fell in relation to the target populations.

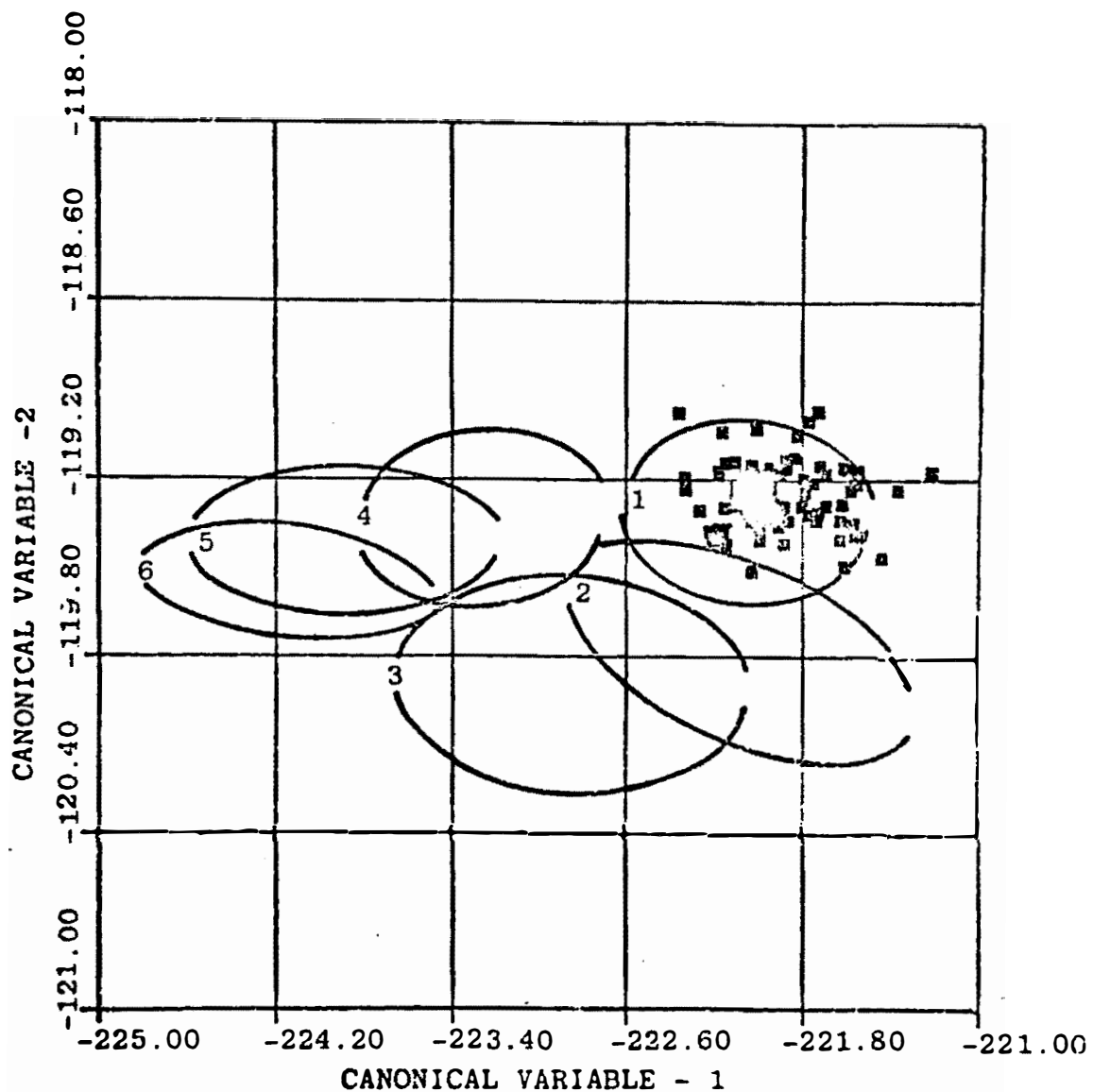
RESULTS

The skulls of 289 canids collected during the study were cleaned. Of these, 53 were too damaged to obtain a complete set of measurements, 46 were pups, and 23 were of unknown sex due to destroyed carcasses or improper labelling. This resulted in 167 skulls from adults of known sex which were suitable for analysis.

Discriminant function analysis indicated that none of the animals examined could be positively classified as anything other than coyotes. Five individuals were of undetermined taxonomic status, and the remaining 162 animals were identified as coyotes. Ninety-four males (15 from Harding County, 46 from Custer and Fall River Counties, and 33 from Gregory and Tripp Counties) and 73 females (12 from Harding County, 37 from Custer and Fall River Counties, and 24 from Gregory and Tripp Counties) were included in the analysis.

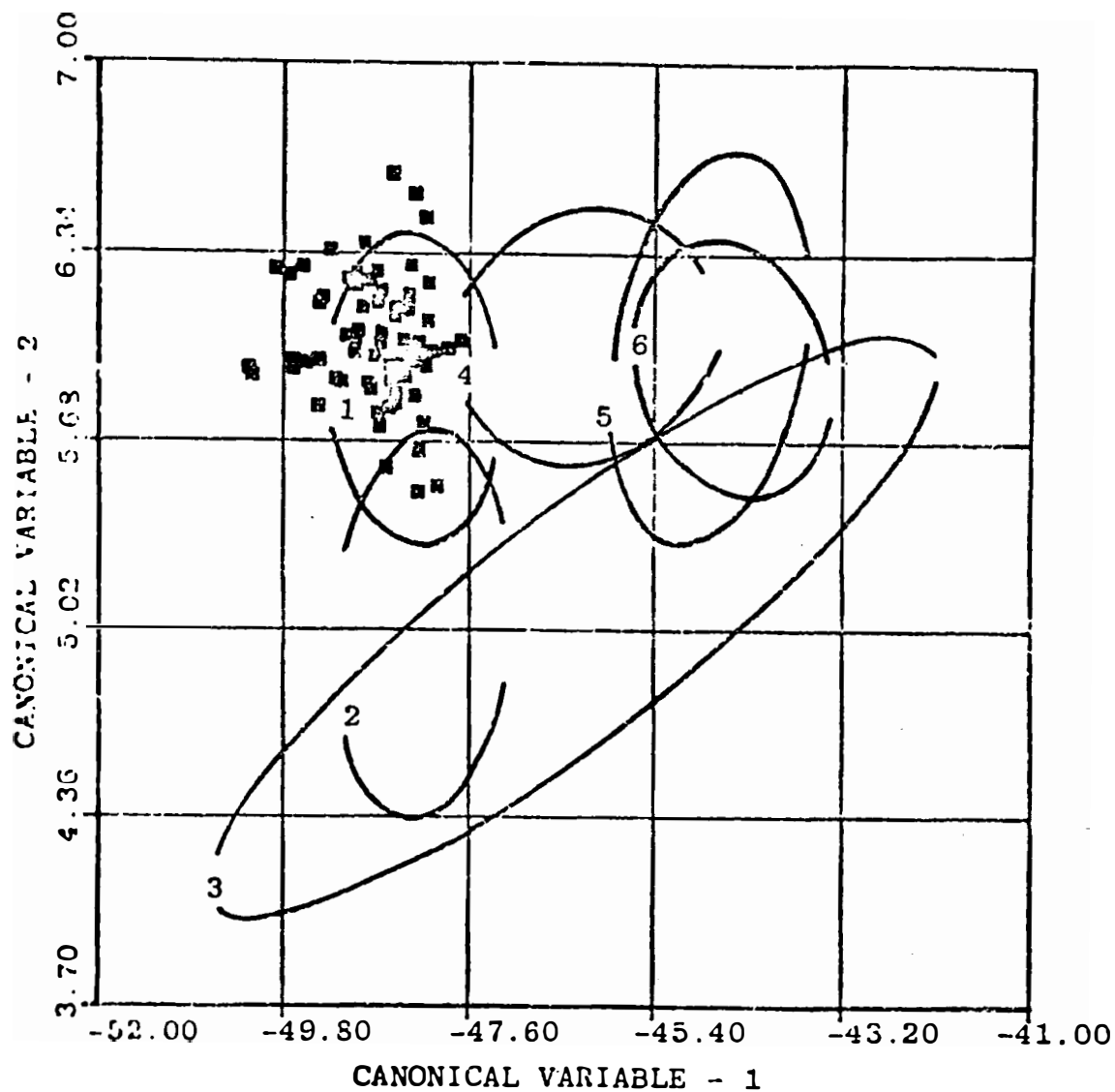
Figures 3 and 4 show the relationships of the specimens analyzed to the target populations. Canonical variables of each specimen have been plotted on a graph showing the 95 percent confidence ellipses of the six target populations. When one of the specimens being analyzed falls within the confidence ellipse of a particular target population, there is a 95 percent chance that it is a member of that population.

Eighty-seven males (92.5 percent) and 50 females (68.5 percent) were well within the 95 percent confidence limits of the coyote target population. These individuals can be positively classified as coyotes. Six males (6.4 percent) and 19 females (26.0 percent) plotted



- 1 MALE COYOTES
- 2 MALE HYBRIDS
- 3 MALE DOGS
- 4 MALE RED WOLVES
- 5 MALE TIMBER WOLVES
- 6 MALE PRAIRIE WOLVES

Figure 3. Canonical variables of male specimens plotted on 95 percent confidence ellipses of target populations (labeled 1 through 6).



- 1 FEMALE COYOTES
- 2 FEMALE HYBRIDS
- 3 FEMALE DOGS
- 4 FEMALE RED WOLVES
- 5 FEMALE TIMBER WOLVES
- 6 FEMALE PRAIRIE WOLVES

Figure 4. Canonical variables of female specimens plotted on 95 percent confidence ellipses of target populations (labeled 1 through 6).

outside the ellipses of all six target populations. The plots of these individuals were mainly clustered around the boundary of the coyote target population, and were all closer to that group than to any of the other targets. For the purpose of taxonomic classification, these specimens were therefore all identified as coyotes.

Among the females, there were four specimens (5.5 percent) that fell in the area of overlap between ellipses of the coyote and coyote-dog hybrid target populations (Figure 4). One male (1.1 percent) was also plotted in this overlap area (Figure 3). These individuals were not positively identified as either coyotes or hybrids. Although it is possible that some or all of these five animals were actually hybrids, I suspect that they were probably coyotes; the lack of any other clearly identifiable hybrids indicates that this may be the case. However, it cannot be stated with certainty that these individuals are either coyotes or coyote-dog hybrids. For the purposes of this study, they are considered unclassifiable.

Examination of the canonical plots showed that the animals from each of the three collection areas were distributed randomly on the graph. That is, individuals from a particular area were not clumped together on the diagram, but rather were interspersed with specimens from all three areas. Computed F values indicated that there was no significant difference ($p < 0.01$) between the measurements of the canids from the three different areas (Tables 1 and 2).

Table 1. Analysis of variance of male canids from the three collection areas; sums of squares and F values for all seven characters measured are shown.

Character	zygomatic width	max. crown width M ²	width across upper cheek teeth	min. crown width PM ⁴	width between PM ¹	width across incisors	canine width
Between group ssq (d.f. = 2)	29.02	0.70	0.29	0.66	0.65	1.93	0.10
Within group ssq (d.f. = 91)	1558.54	32.47	392.76	16.41	123.71	76.91	30.31
F value	0.85	0.98	0.03	1.83	0.24	1.14	0.15

Table 2. Analysis of variance of female canids from the three collection areas; sums of squares and F values for all seven characters measured are shown.

Character	zygomatic width	max. crown width M ²	width across upper cheek teeth	min. crown width PM ⁴	width between PM ¹	width across incisors	canine width
Between group ssq (d.f. = 2)	80.13	0.21	12.76	0.18	1.68	2.95	0.43
Within group ssq (d.f. = 70)	1255.28	25.59	313.89	8.51	112.92	54.84	23.17
F value	2.23	0.29	1.42	0.74	0.52	1.88	0.65

The mean and range of measurements obtained for each of the seven characters is shown in Table 3. Females were generally smaller in all measurements than males, but there was a definite overlap, with some females larger in all measurements than the smallest males.

In no case was any one individual the largest or the smallest in all seven measurements among the animals of the same sex and from the same area. One female from Gregory County, for example, was larger across the zygomatic arch and in the width of the second molar than even the males from that collection area, but she was not the largest of the females in the other measurements. This indicates that although there was a certain amount of variation in the measurements, all were within the size range of normal coyotes.

The Harding County animals showed a narrower range of measurements than did the animals from the other two areas. This may be explained by the relatively smaller sample size from that area.

Table 3. Range and mean of skull measurements for male (N=94) and female (N=73) canids.

Character	Range		$\bar{x} \pm \text{sd}$	
	males	females	males	females
zygomatic width	83.60 - 107.80	83.60 - 105.20	99.15 \pm 4.13	94.46 \pm 4.31
max. crown width M ²	10.55 - 13.45	10.35 - 13.45	12.12 \pm 0.60	11.83 \pm 0.60
width across upper cheek teeth	47.90 - 59.50	46.05 - 57.30	54.33 \pm 2.05	52.03 \pm 2.13
min. crown width PM ⁴	6.05 - 8.30	5.95 - 7.75	7.07 \pm 0.43	6.73 \pm 0.35
width between PM ¹	16.80 - 22.70	16.25 - 21.80	20.12 \pm 1.16	19.31 \pm 1.26
width across incisors	21.65 - 25.50	20.95 - 25.30	23.64 \pm 0.92	22.72 \pm 0.90
canine width	7.45 - 10.60	7.10 - 10.05	9.30 \pm 0.57	8.72 \pm 0.57

DISCUSSION

An increase in hybridization within the genus Canis has resulted from expansion of the range of the coyote (Gipson 1972). Hybridization between coyotes and other canids has occurred most frequently on the fringe of the coyote's range (McCarley 1962, Paradiso 1963, Kolenosky 1971) and in areas only recently inhabited by coyotes (Aldous 1939, Pringle 1960, Silver and Silver 1969, Gipson 1972). Recently, hybrids began appearing in coyote populations that are within the native range of coyotes (Mahan et al. 1978).

Mengel (1971) theorized that the shift in the breeding season which occurs in first generation (F_1) coyote-dog hybrids would make back-crossing with coyotes impossible, and would therefore eliminate the possibility of any second generation (F_2) hybrids. However, research in Arkansas (Gipson 1972) showed that such back-crossing with wild coyotes is possible, and later studies in Oklahoma (Freeman 1976) and Nebraska (Mahan et al. 1978) indicate that it is indeed happening in wild coyote populations. There have also been isolated instances in the past of coyote-dog hybrids in South Dakota, as there are several hybrid skulls in the U. S. National Museum from coyotes that were taken in the state. In view of these facts, it seems likely that some degree of hybridization is taking place in South Dakota coyote populations today, and one would therefore expect to find some evidence of this in a random sample from several populations in the state.

Current wild coyote populations in western South Dakota show no evidence of hybridization with domestic dogs. Of 167 specimens analyzed from three populations, there were no animals which could be positively classified as anything other than coyotes. Further, there is no indication of large scale hybridization occurring in these populations in the past.

The analysis of variance showed no significant difference ($p < 0.01$) between the measurements of the three populations, indicating that the groups are virtually the same taxonomically. Furthermore, examination of the canonical plots showed that each population is taxonomically similar to the others, since each group was scattered randomly on the diagram, rather than clustered in one area. In addition, if all the populations had had a previous history of hybridization, the trend toward hybrid-like characters should have appeared on the canonical plots. Although all specimens might have fallen within the coyote ellipse, there would have been a general shift toward the hybrid ellipse, rather than the more even distribution throughout the coyote ellipse that was found here. It therefore does not appear that there has been any significant hybridization in these populations in the past.

Other studies of coyote hybridization (Gipson 1972, Mahan et al. 1978) have encountered black canids that were morphologically indistinguishable from coyotes; these animals were identified as coyotes. As black coyotes had not been reported in the coyote's native range (Young and Jackson 1951), it was suggested that these melanistic

individuals were the result of previous hybridization to such an extent that true introgression of dog genes into the coyote gene pool had occurred. No black canids were found in the present study; had there been such melanism, earlier hybridization would have to be considered as a possible explanation. The lack of such animals, which were common in the other studies, is a further indication that hybridization with domestic dogs, other than in isolated instances, has not occurred in wild coyote populations in South Dakota.

The three collection areas in this study were located west of the Missouri River (Figure 1), which is generally less populated than the eastern half of South Dakota. Mahan et al. (1978) found most coyote-dog hybrids in areas of relatively high human densities (and therefore higher dog densities). A possible explanation for the lack of hybrids found in the present study is that dog populations are low enough in the study areas that there has been little contact between dogs and coyotes. Yet Gipson (1972) reported that dogs and coyotes frequently associated, even in areas of high coyote populations (and presumably relatively low human and dog populations). Apparently, it is not necessary to have a high human density with a correspondingly high dog population in order to facilitate coyote-dog hybridization. Hybridization can occur wherever dogs come into contact with coyotes. Nor should it be necessary to have an established population of feral dogs before hybridization occurs in the wild. The presence of ranch dogs that are allowed free run should be sufficient to allow encounters with coyotes that could result in hybrid offspring. It is also interesting

to note that one of the collection areas (Custer and Fall River Counties) is the location of vacation homes and tourist facilities, and is not far from a large population center and the state's second largest city (Rapid City). Presumably this should be accompanied by a higher dog density than the other two collection areas, yet this more heavily populated corner of the state also produced no hybrid specimens. The presence or absence of a high density of dogs would not seem to be related in this study to the presence or absence of hybrid specimens.

Two possible explanations for the lack of hybrid individuals in current South Dakota coyote population are: either hybrids are not surviving, or hybridization in western South Dakota is simply not occurring.

The first hypothesis is based on the theories presented by Mengel (1971). Although it does not seem to be true that establishment of a hybrid element in coyote populations is impossible due to the non-synchronous breeding seasons of hybrids and coyotes, Mengel did present a second hypothesis that has yet to be disproven. Matings in the wild between coyote and dog most commonly involve a female coyote and a male dog, as the male dog has a year-round breeding season and would be able to mate with any female coyote in breeding condition. (A male coyote would have to be in breeding season at the same time as a female dog in heat, so it is a less likely combination in the wild.) The first generation hybrid offspring are therefore generally born at approximately the same time of year (late April to mid-May) as coyote

pups, and would have a similar chance for survival. The difficulty in hybrid survival comes with the F_2 generation. Offspring of a hybrid parent, whether one or both parents are hybrids, would be born in the winter between January and mid-March. In areas of extremely harsh winters, there would be a selective disadvantage against pups being born during winter months. Coyote pups are born during the early spring months when there might be an occasional storm, but when the weather is generally beginning to warm up and food is becoming more plentiful. Hybrid pups born during winter months would have to survive both the harsh weather and a relative scarcity of food. Severe winter weather is common on the Great Plains, and South Dakota is farther north than other areas of native range where hybrids have been found in wild coyote populations. A second possibility that would lessen the likelihood of F_2 hybrid survival is the case of the male hybrid parent. The male coyote helps the female in raising the young. The male dog does not assist the female, nor does the male coyote-dog hybrid (Silver and Silver 1969, Mengel 1971). If F_2 pups born in the winter have a hybrid father, they have an even smaller chance of survival, since only one parent (the female) is raising the young. It is possible that the lack of hybrids in the South Dakota population sample is due to failure of F_2 hybrids to survive because of these factors.

The second hypothesis which could explain the lack of hybrids in the population sample is that hybridization between coyotes and dogs is not taking place in South Dakota, outside of isolated instances.

It is probable that significant introgression of dog genes into the coyote gene pool does not occur in native range unless the coyote population has been heavily exploited and kept at extremely low levels. This type of heavy exploitation is difficult, given the limitations placed on control techniques. Connolly and Longhurst (1975) showed in a computer simulation model that it would take extremely heavy kill rates over an extended period of time to significantly reduce coyote populations. That study found that it would take an annual kill rate of at least 75 percent of the breeding population to achieve a sustained decline in coyote population levels. A 50 percent annual kill rate caused coyote populations to stabilize at 72 percent of pre-control numbers after only six years of control. A 75 percent kill rate over 20 years could reduce a coyote population to nine percent of its original breeding population, but the population would recover to pre-control density within five years if control measures were terminated at this point. Even at the 75 percent control level, it would take over 50 years to achieve extermination of the population. Current census techniques for coyote populations are not reliable enough to be able to calculate what level of control is being exerted on a population. It is unlikely that control programs are able to achieve such high levels of population reduction in South Dakota. The manpower and funding available for such a population reduction would be prohibitive to any state or federal agency. It is doubtful that (even considering animals taken by hunting and trapping as well as those removed by government control programs) enough control has been exerted on the

coyote populations of South Dakota to result in extremely low population levels. Thus it seems possible that a large amount of hybridization between coyotes and dogs might not even occur in South Dakota.

Consideration of the hypotheses presented here suggests that the second is the more likely of the two possibilities. Although it is perfectly reasonable to believe that hybrid survival would be low due to births occurring during harsh winter months and to lack of male parental support, this theory does not account for one element: the first generation hybrid. F_1 hybrids would not be facing the same conditions as the F_2 hybrids, and should have a better survival rate, if not one as good as that of coyote pups. F_1 pups might well be lacking male parental assistance, but as the mother would probably be coyote, they would be born at approximately the same time of year as coyote pups, and would not face the severe winter weather in their first days. If a high degree of hybridization were occurring in South Dakota, we probably would not see many (or any) F_2 hybrids that would survive their first spring. But there should still be a number of F_1 hybrids (the result of random matings between coyote and dog) appearing in the population, and some of these should have shown up in our sample.

It can be concluded that, outside of isolated instances, hybridization is not taking place in South Dakota, as there is no evidence of a hybrid element in the wild coyote populations. I can only agree with Nowak (1978) that, even though introgression of dog genes into coyote populations is possible, there is no substantial evidence that

dog genes are leaking into wild coyote gene pools on a large scale. Although hybridization is physically possible and even very probable, it nevertheless is not occurring in South Dakota. The reasons for this lack of hybridization can only be, at this point, pure speculation, and are not within the scope of this research.

LITERATURE CITED

- Aldous, C. M. 1939. Coyotes in Maine. J. Mammal. 20(1):104-106.
- Bee, J. W., and E. R. Hall. 1951. An instance of coyote-dog hybridization. Trans. Kans. Acad. Sci. 54(1):73-77.
- Benirschke, K. 1967. Sterility and fertility of interspecific mammalian hybrids. pages 218-234 in K. Benirschke, ed. Comparative aspects of reproductive failure. Springer-Verlag, New York.
- Connolly, G. E., and W. M. Longhurst. 1975. The effects of control on coyote populations: a simulation model. Univ. Calif. Coop. Ext. Bull. 1872. 37pp.
- Cook, R. 1952. The coy-dog: hybrid with a future? J. Hered. 43(2):71-73.
- Dice, L. R. 1942. A family of dog-coyote hybrids. J. Mammal. 23(2):186-192.
- Freeman, R. C. 1976. Coyote x dog hybridization and red wolf influence in the wild Canis of Oklahoma. M. S. Thesis. Oklahoma State Univ., Stillwater. 62pp.
- Gier, H. T. 1968. Coyotes in Kansas. Kansas State Univ. Agric. Exp. Stn. Bull. 393. 118pp.
- Gipson, P. S. 1972. The taxonomy, reproductive biology, food habits and range of wild Canis (Canidae) in Arkansas. PhD. Thesis. Univ. Arkansas, Fayetteville. 188pp.

- _____, I. K. Gipson, and J. A. Sealander. 1975. Reproductive biology of wild Canis (Canidae) in Arkansas. J. Mammal. 56(3):605-612.
- _____, J. A. Sealander, and J. E. Dunn. 1974. The taxonomic status of wild Canis in Arkansas. Syst. Zool. 23(1):1-11.
- Hall, E. R. 1943. Cranial characters of a dog-coyote hybrid. Am. Midl. Nat. 29(2):371-374.
- Howard, W. E. 1949. A means to distinguish skulls of coyotes and domestic dogs. J. Mammal. 30(2):169-171.
- Iljin, N. A. 1941. Wolf-dog genetics. J. Genetics. 42(3):359-414.
- Jolicoeur, P. 1959. Multivariate geographical variation in the wolf Canis lupus L. Evolution 13(3):283-299.
- Kennelly, J. J., and J. L. Roberts. 1969. Fertility of coyote-dog hybrids. J. Mammal. 50(4):830-831.
- Kolenosky, G. B. 1971. Hybridization between wolf and coyote. J. Mammal. 52(2):446-449.
- Lawrence, B., and W. H. Bossert. 1967. Multiple character analysis of Canis lupus, latrans, and familiaris, with a discussion on the relationship of Canis niger. Am. Zool. 7(2):223-232.
- _____, and _____. 1969. The cranial evidence for hybridization in New England Canis. Breviora 330:1-13.
- Linhart, S. B., and F. F. Knowlton. 1967. Determining age of coyotes by tooth cementum layers. J. Wildl. Manage. 31(2):362-365.
- Mahan, B. R., P. S. Gipson, and R. M. Case. 1978. Characteristics and distribution of coyote x dog hybrids collected in Nebraska. Am. Midl. Nat. 100(2):408-415.

- McCarley, H. 1962. The taxonomic status of wild Canis (Canidae) in the south central United States. Southwestern Nat. 7(3/4):227-235.
- Mengel, R. M. 1971. A study of dog-coyote hybrids and implications concerning hybridization in Canis. J. Mammal. 52(2):316-336.
- Nowak, R. M. 1978. Evolution and taxonomy of coyotes and related Canis. pages 3-16 in M. Bekoff, ed. Coyotes: biology, behavior, and management. Academic Press, New York.
- Paradiso, J. L. 1968. Canids recently collected in east Texas, with comments on the taxonomy of the red wolf. Am. Midl. Nat. 80(2):529-534.
- Pringle, L. P. 1960. Notes on coyotes in southern New England. J. Mammal. 41(2):278.
- Rao, C. R. 1952. Advanced statistical methods in biometric research. John Wiley and Sons, Inc., New York. 390pp.
- Richens, V. B., and R. D. Hugie. 1974. Distribution, taxonomic status, and characteristics of coyotes in Maine. J. Wildl. Manage. 38(3):447-454.
- Silver, H., and W. T. Silver. 1969. Growth and behavior of the coyote-like canid of northern New England with observations on canid hybrids. Wildl. Monogr. 17:1-41.
- Young, S. P., and H. H. T. Jackson. 1951. The clever coyote. Stackpole Co., Harrisburg, Pa., and Wildl. Manage. Inst., Washington, D. C. 411pp.